THE SUBORDERS OF DIPTERA

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ABSTRACT—The higher classification of the Diptera is considered, with special reference to the recent classification proposed by Boris Rohdendorf. A redeployment of the families of Diptera into three major groups, which may reflect more of a natural evolutionary pattern than the conventional Suborders is proposed. These are the Suborders Superstata, Madescata, and Arescata.

"A critical examination of all existing schemes proposed during the 150 years of study of the Diptera shows that most of them were based upon either a single feature or a group of structural characteristics. Each author proposing and defending his own system has usually not attempted to evaluate the categories that he was establishing in any ecological or ethological sense". Rohdendorf (1974, p. 17).

The student is told that Diptera are classified into three Suborders, but he is given only unsatisfactory reasons for making these divisions. The explanation by Imms (1957, p. 607) is typical, "The Diptera may be classified into three suborders, viz. the Nematocera, Brachycera and Cyclorrhapha. The first mentioned include the most primitive forms, the Cyclorrhapha comprise the most highly specialized while the Brachycera occupy in some respects a position intermediate between these two groups. In the time-honoured classification of Brauer two suborders are recognized, viz. the Orthorrhapha (including the Nematocera and Brachycera) and the Cyclorrhapha. These differ rather in the absence or development of a puparium than in the method by which the imago escapes from the pupa, the feature stressed by Brauer."

Then follow summaries of characters for the three Suborders, but with many qualifications and exceptions. The aforesaid student, therefore, cannot run down an unknown fly in any systematic way, but must wait until he is familiar with the appearance of at least the larger families.

Other authors have attempted to construct keys that would lead directly to the Suborders. Thus Colless and McAlpine (1970, pp. 678–679) make a primary division into Nematocera and Brachycera, further dividing the latter into Orthorrhapha and Cyclorrhapha, but the characters used are full of hesitations and qualifications. The first half of the first couplet, defining Nematocera, includes the words 'relatively', 'often', 'rarely more or less', 'usually (rarely reduced)', 'rarely', 'often', 'except in some . . .', and 'mostly'—all in five lines of print.

This is a commentary on the insects, not the authors. In the same

year I attempted to do the same thing (Oldroyd, 1970, p. 65), starting at the other end of the Order, and first eliminating all the flies with a ptilinal suture as Cyclorrhapha-Schizophora. This is a step forward, but the further analysis into Nematocera, Brachycera and Cyclorrhapha-Aschiza is just as unconvincing as those of other authors. On an earlier page (1970, p. 63) I glossed over this difficulty with the bland phrase: "In practice one seldom needs to use the keys to determine the Suborders . . ."

One wonders, therefore, whether the 'time-honoured classification' into Nematocera, Brachycera and Cyclorrhapha serves any useful purpose. It was with some curiosity on this point that I approached Rohdendorf's book *The Historical Development of the Diptera*, the English translation of which has now appeared, and which I had the privilege of seeing during its editorial stages.

Rohdendorf recapitulates the Nematocera/Brachycera and Orthorrhapha/Cyclorrhapha divisions, discussing their validity (pp. 18–20), and reaches the familiar conclusion that: "Only Nematocera on the one hand and Cyclorrhapha in the narrow sense on the other, can be formally defined. 'Brachycera' and 'Orthorrhapha' overlap with these, because Brachycera includes both orthorrhaphous and cyclorrhaphous forms, while Orthorrhapha may be either nematocerous or brachycerous." Nor does internal anatomy give any clearer guidance. Neither the number of Malpighian tubules nor the structure of the vascular system is consistent with either of the two customary divisions of the Order. Hence: ". . we can draw certain quite definite conclusions. The suborders Nematocera, Brachycera-Orthorrhapha and Cyclorrhapha, as they are widely accepted by almost all taxonomists, *are not natural groups*" (my italics).

The last four words are the important ones. As long as we believe that the three Suborders bring the Diptera into groups of naturally related families we can accept the difficulty of precisely defining them. Indeed this is what we should expect when we are attempting to subdivide such a diverse Order of insects. If, however, these Suborders can neither be adequately defined nor believed in, then what use are they?

In an earlier paper addressed to the XIth International Congress of Entomology Rohdendorf (1961) had separated off the strange family Nymphomyiidae as sole representative of the Suborder Archidiptera, and lumped all the rest into the single Suborder Eudiptera. In effect he abandoned any attempt to form Suborders, and classified Diptera directly into thirteen *infraorders*, each named after a typical family: thus *Bibionomorpha*.

Since my working life has been spent studying the taxonomy of the Brachycera-Orthorrhapha I looked with particular attention at these families, and found that Rohdendorf retained them in a single infra-

order, Asilomorpha. This is not consistent with my own conclusions, which are based upon biological as well as structural considerations, as advocated by Rohdendorf himself in the passage quoted at the head of this article. By a coincidence, in the same year (1964) as the original Russian text of Rohdendorf's book appeared, I published a book called *The Natural History of Flies* in which I attempted to trace an evolutionary pattern in the biology and life-history of the various groups of Diptera. I arrived at the general conclusion that: "It seems to me more helpful to look upon the larva as an ancillary stage, relieving the adult of most of the laborious and protracted feeding needed during the life of an individual. Those adults that have continued in the primitive bloodsucking habit like the mosquitoes and blackflies, and those that have reverted to predaceous or bloodsucking habits like the robber-flies and tsetse-flies, are thereby supplementing an inadequate diet. In other words the adults, where necessary, make up for the deficiencies of the larva, not the opposite." (Oldroyd, 1964, p. 25).

This same theme is central to Rohdendorf's book, and constitutes the 'conflict' that he envisages as having to be resolved during the evolution of every family of flies. For example: ". . . insufficiency of larval food was one of the oldest problems to arise in the evolution of Bibionomorpha" (p. 64), and again, speaking of the Fungivoridea (p. 65): "These features suggest that the chief evolutionary problem to be overcome was once again insufficiency of larval food, leading to perfection of the winged phase." Most taxonomists will study *The Historical Development of Diptera* to see which of their favourite families are merged, or (more often) split up, but these decisions are personal, and ephemeral, and are already more than ten years out of date. The lasting contribution of Rohdendorf's book lies in his illuminating comments on the implied way of life of the Diptera of the past, and its relevance to the composition of the surviving fauna. Can we not apply this method, using a combination of structural and ecological data, to suggest some major subdivision of the Eudiptera that will be more meaningful than the traditional three Suborders?

The grouping of all the families of Brachycera-Orthorrhapha into one infraorder Asilomorpha obscures the very obvious differences that exist between the families related to Tabanidae, Rhagionidae and Stratiomyidae, and all the rest. Indeed, if we stand, as it were, at this center point of the Order Diptera, we look backwards with Tabanidae and others into the Nematocera, and forwards with Asilidae and Bombyliidae into the higher Diptera. It was from this viewpoint that I divided the Brachycera-Orthorrhapha of the British fauna into two superfamilies only, Tabanidea and Asilidea (Oldroyd, 1969, p. 2), and suggested that Tabanidea should be compared with the 'watery', bloodsucking groups of Nematocera rather than with the Asilidea.

Certainly there are differences, both adult and larval, between Tabanidea and Culicimorpha, but there are two significant points of resemblance; they have predominantly aquatic larvae, and Rhagionidae and Tabanidae, at least, have many mandibulate, bloodsucking females. There have long been arguments whether the latter is a persistence of an archaic habit, or whether it has arisen many times independently during the evolution of Diptera. I believe that it has arisen only once, and that therefore all groups which include mandibulate, bloodsucking females are descended from a single stock. I believe this because the mandibulate, piercing mouthparts are so essentially similar in all the families in which they occur. There are many examples of the *loss* of mandibles even in particular genera and species (e.g. *Sphecodemyia* in Tabanidae), but no known example of a parallel development of mandibles. From Asilidae onwards piercing and bloodsucking occurs sporadically, and by means of entirely new equipment; in Asilidae and Empididae based upon the hypopharynx, in Dolichopodidae and some Muscidae by a combination of crushing labella and either prestomal or pseudotracheal teeth. Similarly, in these families from Asilidae onwards, when aquatic larvae occur, as in Syrphidae and Ephydridae, this can be explained as secondary migration to water by essentially terrestrial stocks. At no point anywhere near to these families can one trace an aquatic ancestry.

It seems, therefore, that relationships among the families of Diptera would be better understood if the grouping of Brachycera-Orthorrhapha were to be abandoned, but this could hardly be done by simply assigning Tabanidea to 'Nematocera' and Asilidea to 'Cyclorrhapha'. New terms would be needed, and might be associated with a fundamental rearrangement. The concept of 'Nematocera' is handy because it is easily understood ('threadhorns'), but difficulty has always arisen because a number of primitive 'Brachycera' have multisegmented antennae: e.g. *Rhachicerus*, and many Stratiomyidae, and in existing keys we have to resort to subterfuges such as the vagaries of the anal vein to justify excluding these from Nematocera.

Rohdendorf repeatedly stresses the disparity between two main lines of evolution among Nematocera, and concludes (p. 24) that: "On the whole therefore, the suborder 'Nematocera' does not possess any real unity, but consists of an assembly of groups of superfamilies not directly related to one another. He does, however, recognise some degree of grouping into 'Oligoneura', centering around Bibionidae, and 'Polyneura' centering around Culicidae. These are what I have called the 'earthy' and 'watery' groups respectively. I applied these names, rather than 'terrestrial' and 'aquatic', to avoid the natural criticism that both groups include many Diptera the larvae of which live in intermediate habitats, neither terrestrial nor aquatic: e.g. in the debris in a rot-hole in a tree. Yet I think that there is a real distinction

between them, once we have left behind the Tipulidae and a few closely related families, where there is still such a wide range of larval habitats that we can only regard them as preserving, as it were, an ancestral uncertainty of evolutionary direction.

I suggest, therefore, that we should again group the superfamilies of Diptera into three Suborders, but radically different from the traditional ones, and based upon general ecology and habits, rather than directly on structural grounds. These would be:

1. Tipulidae and those related families that can be regarded as relicts from the original basic group of Diptera (Oldroyd, 1964, pp. 29–40). They would comprise the superfamilies Pachyneuridea and Tipulidea of Rohdendorf (1964, 1974, p. 9). Suggested name: Suborder SUPERSTATA, from *superstes*, surviving.

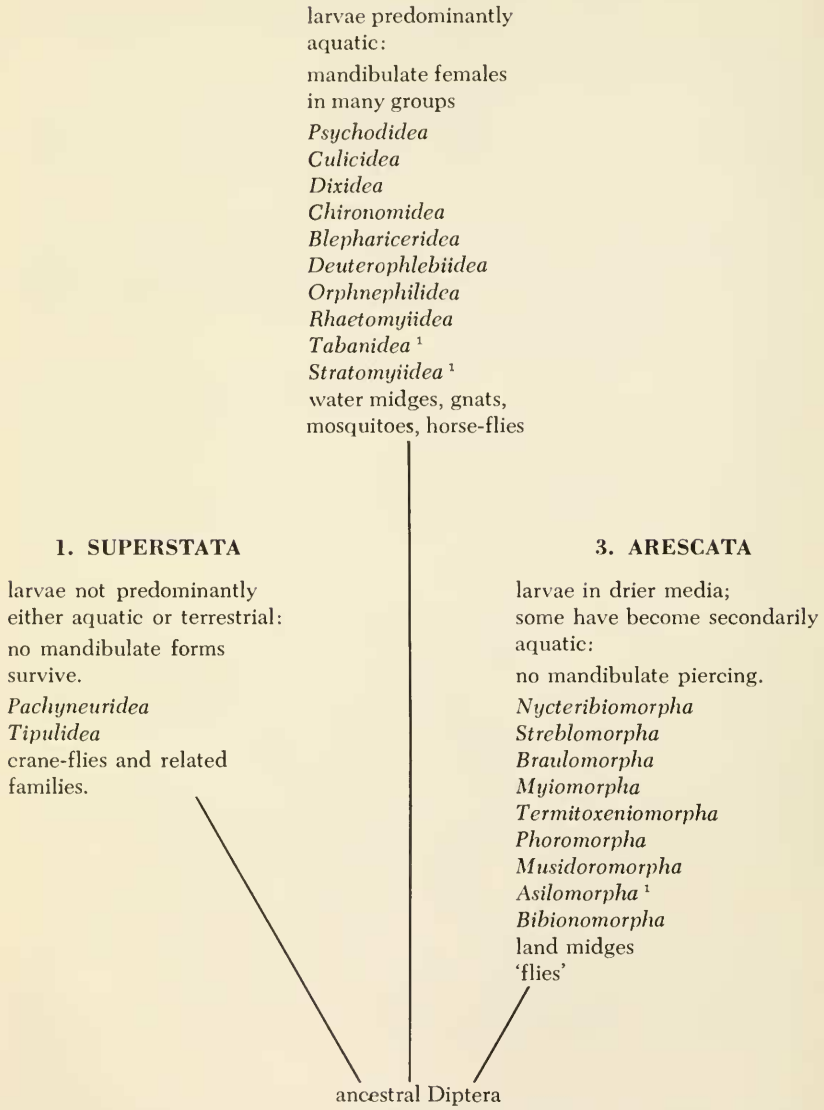
2. All the 'watery' families, with characteristically aquatic larvae, and including all those with any mandibulate, bloodsucking females. Superfamilies Psychodidea, Culicidea, Dixidea, Chironomidea, Orphnephilidea and Rhaetomyiidea of Rohdendorf (1964, 1974, pp. 9–10) *plus* Tabanidea and Stratiomyiidea (ibid, p. 11). Suggested name: Suborder MADESCATA, from *madescere*, to become moister, to tend towards wetness.

3. All the rest of Diptera, which are essentially terrestrial, even though some of them have secondarily returned to water as a larval habitat. When they have also re-acquired the bloodsucking habit, this is carried out by other structures than mandibles, and is common to both sexes. This Suborder includes the 'earthy' groups of 'Nematocera', and all the Diptera from Asilidae onwards: suborders Bibionomorpha, Asilomorpha (less Tabanidea and Stratiomyidea), Musidoromorpha, Phoromorpha, Termitoxeniomorpha, Myiomorpha, Braulomorpha, Streblomorpha, Nycteribiomorpha of Rohdendorf (1964, 1974, pp. 10–14).

Suggested name: Suborder ARESCATA, from *arescere* to dry up.

Rohdendorf sets up separate infraorders for the two families of 'mountain midges', Blephariceridae and Deuterophlebiidae. There are no known fossils of these, but the evidence of the living forms, adults and larvae, leads him to associate each of them with his superfamily Chironomidea. This would place them in the Madescata of our grouping.

Three families of Rohdendorf's Asilomorpha call for special mention. It will be noted (p. 11) that he assigns Nemestrinidae to Tabanidea and Acroceridae to Stratiomyiidea. Because these two families have a padlike empodium ('three pulvilli') they have traditionally been placed in Hendel's Homeodactyla, in contrast to Asilidae and the rest which have the empodium bristlelike, and were classed as Hetero-



[1] with the exceptions discussed in the text

dactyla. I think that this is a superficial and misleading association, and an example of the excessive reliance on a single structural character against which Rohdendorf himself has warned us. It seems to me that both adult and larval characters relate these two families to Bombyliidae (Oldroyd, 1964, p. 134; 1969, p. 107), and hence they should be removed to Rohdendorf's superfamily Bombyliidea, where he has split Bombyliidae in the usual sense into four families (Bombyliidae, Usiidae, Cyrtosiidae and Systropodidae). This is in accord with many current workers on this group, who consider that these groups are too disparate to be retained in one family. There is, as yet, no consensus of opinion as to the details of this fragmentation, and I suggest that Nemestrinidae and Acroceridae should also be considered as part of this complex.

A third problematical family is Scenopinidae, which have been closely linked with Therevidae because their larvae are at once so similar and so unlike any others of the Asiloidea. Therevidae seem correctly placed close to Asilidae, but I have long thought that Scenopinidae are more like Stratiomyidae, especially about the head (Oldroyd, 1969, p. 104). Rohdendorf (p. 88) refers to them as 'the relict family Scenopinidae, which out of the contemporary Asilidea is probably the group most closely related to the original form of the subfamily'. I would go further, and suggest that they may be regarded as a terrestrial offshoot of Stratiomyiidea, perhaps analogous to Vermileoninae, which are a terrestrial offshoot of Rhagionidae, and which some authors would segregate into a distinct family.

The object of the present paper is to suggest a redeployment of the families of Diptera into three major groups, which may reflect more of a natural evolutionary pattern than the conventional Suborders. For this purpose I have used the superfamily names employed by Rohdendorf (1964, 1974), and to facilitate reference to his book I have retained the unusual ending *-idea*. Apart from what I have said above, I express no views about the assembly of families within these superfamilies. This is a very big question, and no two authors agree, as will be seen by comparing Rohdendorf's list with those of Imms and the *Insects of Australia*.

There is however, a growing measure of agreement among dipterists for the overall pattern, and it is hoped that the suggestions given in this paper, may contribute to this. We may end, as we began, with a quotation from Rohdendorf (p. 290): "The further history of the Diptera i.e. after Lower Triassic times consists, in fact, only of the fortunes of two of the infraorders—the aquatic tipulomorphs [i.e. my Superstata + Madescata] and the terrestrial bibionomorphs [my Arescata] . . . which gave rise to the younger infraorders widespread in the Cenozoic".

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NOTE

THE TAXONOMIC STATUS OF PORTACHORUTES WRAY (COLLEMBOLA: NEANURIDAE)

The genus *Portachorutes* was erected by Wray (1953, J. Agr. Univ. P. R. 37: 140–150) for the Puerto Rican species *Portachorutes mambatus*.

Massoud (1967, Biol. Amer. Australe. 3: 1–399) and Rapoport (1971, Pacif. Ins. Mon. 25: 99–118) regarded this monotypic genus as of dubious taxonomic status. The former author omitted the genus from his monograph of the Neanuridae (first reference above). On the other hand, Salmon (1964, Bull. Roy. Soc. New Zealand. 7: 1–651) and Mari Mutt (1976, J. Agr. Univ. P. R. 60: 113–128) regarded the genus as valid.

A detailed study of specimens collected in Puerto Rico has shown that *Portachorutes* is a synonym of the genus *Arlesia* Handschin (1942, Ver. Naturf. Ges., Basle. 53: 265–284) since *P. mambatus* is a synonym of *A. albipes* Folsom (1927, Proc. U. S. Nat. Mus. 72: 1–16), the type species of *Arlesia*. The Puerto Rican specimens, in addition, fit well the redescriptions of the latter species furnished by Denis (1931, Boll. Lab. Zool. Portici 25: 69–170) and Massoud (1963, Stud. Fauna Surinam and other Guyanas. 6: 43–51).

Due to the great value of Massoud's 1967 monograph, I find it desirable to publish the aforementioned synonymies in order to fill this gap in the cited work.

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